The spawn and embryonic development of colour variants of *Dendrodoris nigra* Stimpson (Mollusca: Nudibranchia)

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ABSTRACT

Colour variants of *Dendrodoris nigra* from New South Wales produce morphologically different planktotrophic larvae. All colour variants deposit transparent gelatinous egg ribbons which are arranged spirally onto hard substrata. Embedded into the matrix of the ribbons are yellow zygotes. Colour variants which are brownish-black, gray or black with white speckles (form 1) can produce up to 251,000 zygotes (diameter 74-75 μm) per spawn. Form 1 embryos hatch 9.6 days after oviposition at 22-23°C. Newly liberated veligers (mean length 114 μm) are shaped like most planktotrophic opisthobranch larvae; each veliger has a transparent sinistrally coiled shell, operculum, hyperstrophically arranged visceral mass and a cephalopedal region which can be retracted into the shell. The subvelum of form 1 veligers is not well defined like that of form 2. Colour variants which are jet-black or black with red-rimmed mantles (form 2) produce up to 88,600 zygotes per spawn. Zygotes of jet-black variants (mean diameter 129 μm) are significantly larger ($P < 0.05$, Student's t-test) than those of variants with red-rimmed mantles (mean diameter 121 μm). Differences in diameter of zygotes have no effect on the shape of the veligers. Form 2 embryos hatch 9.2 days after oviposition at 22-23°C. Mean shell length of newly liberated veligers produced by jet-black variants is 153 μm, 9 μm greater than that of veligers produced by variants with red-rimmed mantles. Compared to most planktotrophic opisthobranch larvae, the shape of form 2 veligers is atypical in that each lacks an operculum and possesses an oversized cephalopedal region which can not be retracted into the shell. The shell of form 2 is darkly pigmented when embryos are reared in the laboratory. Colour variants do not appear to vary their developmental mode and in the laboratory copulation occurs only between individuals with the same colour pattern. Differences in larval morphology suggests that certain colour variants of *D. nigra* may be separate (sibling) species.

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INTRODUCTION

Dendrodoris nigra Stimpson, 1856 is a sponge-eating (Bloom, 1976), Indo-Pacific nudibranch found along the east and west coasts of Australia (Allan, 1947; Thompson, 1975; Roberts & Wells, 1980). Adults of this species from east Africa and India are known to vary in colour, texture of the mantle and in number of branchiae (Gohar & Soliman, 1967; Narayanan, 1968). Specimens from New South Wales also display variations in colour that are comparable to those recorded from other regions of Australia (Allan, 1947; Burn, 1969), Hawaii (Kay & Young, 1969), Egypt (Gohar & Soliman, 1967) and Tanzania (Edmunds, 1971). As in Hawaii (Kay & Young, 1969), colour variants of *D. nigra* from New South Wales produce planktotrophic larvae which hatch from egg-mass ribbons deposited on hard substrata. The shape of the spawn and patterns of embryogenesis, however, differ for certain colour morphs.

In this paper the egg masses and larval development of several colour variants of *D. nigra* from New South Wales are described for the first time and compared with those of its congeners. Discrepancies in spawn and embryogenesis suggest that separate (sibling) species might exist.

MATERIALS & METHODS

All nudibranchs collected matched the descriptions recorded for *D. nigra* by Allan (1947) and Thompson (1975). Specimens taken intertidally at Long Reef, Sydney during 1976 to 1979 were either black with white-speckled dorsal surfaces, gray or brownish-black (Table 1). Specimens taken intertidally at Pilot Beach, Laurieton during 1979 were jet-black with the inside edge of the mantle skirt outlined in red and specimens collected intertidally at Bottle & Glass, Sydney and subtidally at Clovelly, Sydney during 1979 were jet-black (Table 1).

Animals were brought back to the laboratory and kept in aquaria. Egg masses produced in the laboratory or collected in the field were placed in glass bowls filled with filtered seawater at 22-23° and 33-34‰S. Larvae were fed unicellular phytoplankton *(Pavlova lutheri, Isochrysis galbana* and *Phaeodactylum tricornutum)* but failed to grow and died after ten days.

Observations on developmental patterns of each colour variant were made with a phase contrast microscope. Photographs were taken with a camera and flash unit attached to the microscope. Morphometric characteristics of the zygotes, capsules and veligers of different colour variants were analyzed with either a paired Student's t-test or balanced one-factor analysis of variance (ANOVA). Significant differences between colour variants were further tested a posteriori with a Student-Newman-Keuls (SNK) multiple comparison test (Sokal & Rohlf, 1969).

Nudibranchs which were black and speckled, gray or brownish-black always produced identical spawn and embryos, and will be referred to as *D. nigra* (form 1). Except for differences in the sizes of the spawn and eggs, colour morphs which were jet-black or red along the edge of the mantle produced identical embryos, and will be referred to as *D. nigra* (form 2).

RESULTS

Spawn

In the laboratory copulation occurs only between specimens with the same colour pattern. Egg masses produced by both forms are Type A (as defined by Hurt, 1967) or a_1 (as defined by Fernandez-Ovies, 1981) and are similar to those recorded for *Dendrodoris gemmacea* by Baba (1956) and Rose (1981) and *D. fumata* by Gohar & Soliman (1967). Except for nudibranchs with red-rimmed mantles, all other colour morphs deposit spirally coiled, transparent ribbons with double-membraned egg capsules unevenly packed two or three layers deep within the gelatinous matrix of each ribbon. Egg masses produced in the laboratory by these nudibranchs are identical to those collected in the field.

Only one egg mass produced by nudibranchs with red-rimmed mantles was observed. The ribbon was similar to the others except that it was smaller and deposited in a semi-circular rather than spiral pattern. Whether this semi-circular configuration is typical or the result of the laboratory conditions was not determined.

Each egg capsule generally encases one yellow or brownish-yellow zygote but form 1 egg ribbons can contain anything up to 11 zygotes per capsule. Capsules encasing more than two zygotes are tubular, enclosing a single row of zygotes and oriented vertically with respect to the attached edge of the ribbon (Plate 1, A). Form 1 egg ribbons are more flaccid than those of form 2 and often have as many as three grooves running lengthwise along the ribbon. These grooves caused by uneven spacing of capsules within the ribbon matrix, occur when a monolayer of capsules is present or when gaps exist within the layers of capsules.

For both forms 1 and 2, the total number of zygotes contained within an egg ribbon varies with the length of ribbon. The mean number per ribbon produced by form 1 is generally three or four times greater than that produced by form 2 (Table 1). Under laboratory conditions, a 220 mm long ribbon deposited by a white-speckled *D. nigra* (form 1) will contain up to 242,850 zygotes while a 120 mm long ribbon deposited by a jet-black *D. nigra* (form 2) will contain 67,584. The total number of zygotes produced by nudibranchs with red-rimmed mantles was not calculated but it is estimated to be tens of thousands for spawn ranging from 60 to 70 mm in length.

Mean diameters of the zygotes and capsules of form 1 colour morphs, form 2 (red-rimmed mantle) and form 2 (jet-black) are as follows: 74-75 and 121-122 μm; 121 and 140 μm; and 129 and 163 μm, respectively (Table 1). Zygotes produced by nudibranchs with red-rimmed mantles are significantly smaller than those belonging to jet-black specimens (t-test: $t=5.25 > t_{0.05}=2.038$; $P < 0.05$). However, they are significantly larger than those belonging to form 1 colour morphs (t-test: $t=6.896 > t_{0.05}=2.548$; $P < 0.05$). The capsule size of the zygotes of different colour morphs are significantly different (one-factor ANOVA: $F4, 45=5.04$; $P < 0.01$). A SNK test indicates that the mean sizes of form 1 and form 2 (red-rimmed mantle) are not significanty different from each other ($P > 0.05$) but that they are all significantly smaller ($P < 0.05$) than capsules produced by form 2 (jet-black).

Development

For either form, there is no difference in the development of embryos from egg masses laid in the laboratory or collected from the field. Embryos of forms 1 and 2 take between 9 and 9.6 days to hatch when incubated at 22-23°C (Table 1). The timing of different stages of development are listed in Table 2. Photographs of a number of these stages are shown in Plates 1 and 2.

Early development to trochophore (Plate 1, A to D)

Except for differences in the size of zygotes, early development up to the trochophore stage or embryogenesis in embryos of either colour form is similar and comparable to that described for other nudibranchs (e.g., Casteel, 1904; Thompson, 1976; Rose, 1981). Briefly, first and second cleavage are equal, holoblastic and meridional (Plate 1, A and B). Cleavage beyond the two cell stage is spiral and at the eight cell stage formation of the first set of micromeres is asynchronous (Plate 1, B). The micromeres at this stage are displaced dexiotropically with respect to their blastomeres. During the blastula stage embryos are flattened dorso-ventrally. By the second day after oviposition they are at gastrula.

The process of gastrulation is a mixture of invagination and epiboly, resulting in a ventrally positioned blastoporal cleft along the sagittal plane of the embryo. At this stage form 1 and 2 embryos appear heart-shaped (Plate 1, C and D). Gradually the cleft disappears except antero-ventrally where it forms a circular depression of lightly coloured cells (the blastopore), marking the future site of the stomodoeum. Towards the end of gastrulation, the anal cells on a number of form 2 embryos can be seen postero-ventrally and to the left of the sagittal plane; anal cells are not observed on form 1 embryos at this stage.

The morphology of form 1 and 2 embryos begins to differ at the trochophore stage. Although both forms develop a slow arhythmically beating prototroch and a shell gland, form 1 embryos still fail to display a pair of anal cells or a thin protruding rudimentary metapodium like that obvserved in form 2.

Early, middle and late veliger stages (Plate 1, E and F; Plate 2, A and B)

The first signs of bodily movement occur at the early veliger stage for embryos of both forms. Although shaped differently, form 1 and 2 embryos at this stage possess a stomodoeum, rudimentary velum and metapodium and a pair of anal cells, situated mid-ventrally just beneath the metapodial rudiment. Their visceral mass is still undifferentiated and opaque from large amounts of yolk. When viewed laterally, the shell gland of embryos of both forms is positioned mid-dorsally and can be seen as a long slightly raised mound of translucent cells.

Form 1 embryos at the early veliger stage display a darkly pigmented mass of cells which is located posteriorly on the left side, just beneath the surface of the body (Plate 1, E). Whether this pigmented mass of cells is the secondary (embryonic) kidney as described in other opisthobranchs (Thompson, 1958; Bridges, 1975; Bonar, 1978) was not determined. However, during the later stages of development the mass moves to the right side, beneath the anus and develops either into two large empty cells or remains darkly pigmented. Form 2 embryos at this stage typically have polar bodies adhering to the outer edges of their stomodoeum which consists of a deep depression of semi-transparent cells (Plate 1, F).

Form 1 and 2 embryos begin rotating during the middle veliger and at this stage their mantle and shell have advanced enough to completely enclose the visceral mass. Form 1 embryos at the beginning of the middle veliger stage have no mantle cavity, statocysts or pedal glands but like form 2, the anal cells towards the end of this stage have reached their definitive position ventro-laterally on the surface of the right side of the embryo. The rudimentary velum of form 2 becomes bilobed at this stage and the metapodium develops two statocysts. This does not occur in form 1 until the late veliger stage.

Towards the end of the middle veliger stage the visceral mass of form 2 embryos differentiates into an alimentary tract. The oesophagus is short and straight and attached to the stomach antero-dorsally. The stomach is opaque and partially obscured from view by the digestive diverticula and a large translucent vesicle located posteriorly on the left side of the embryo, between the left digestive diverticulum and stomach. In form 1 embryos, a translucent vesicle of this kind is not observed. Although both digestive diverticula of form 2 are still filled with yolk at the middle veliger stage, the left is twice as large as the right. The hindgut is a dark narrow tube which is slightly wider at the beginning where it leaves the stomach postero-dorsally. It loops over the dorsal region of the embryo to the right side and traverses over the top of the secondary (embryonic) kidney until it opens into the mantle cavity through the anus, near the two anal cells. The secondary kidney of form 2 embryos at the middle veliger stage appears as a large, dark mass of cells located in the right dorso-lateral region of the embryo, at the base of the velum. As in *D. fumata*, it is a large oval structure and is multicellular in composition (Gohar & Soliman, 1967). The final fate of the secondary kidney was not determined because unfortunately the shells of form 2 embryos become too opaque for external observations beyond the middle veliger stage. The nephrocysts could not be found but they are probably adjacent to and left of the secondary kidney, as described for *D. fumata* by Gohar & Soliman (1967).

The transition between the middle and late veliger stages is more subtle in form 2 embryos than in form 1 as their visceral mass has already become fully differentiated by the end of the middle veliger stage. Moreover, as stated above, detection of the late veliger stage in form 2 is confounded by the intense pigmentation of the shell which prevents viewing of the final position and state of the visceral organs. According to Gohar & Soliman (1967), the degree of opaqueness of the larval shell of *D. fumata* is directly related to the intensity of light to which embryos are exposed. Whether or not this is the case with *D. nigra* (form 2) was not tested. Larval shells of *D. nigra* (form 1) do not become pigmented.

Morphogenesis of the cephalopedal region is the only event distinguishing the late veliger stage from the middle veliger in form 2 embryos. During the late veliger stage, velar lobes of form 2 embryos grow larger and develop well-defined subvela (Plate 2, B and D). Unlike form 1, the cephalopedal region becomes so large that the embryos are unable to retract into their shells. Their transparent velar lobes are composed of large refringent granules and are provided, along the outside edge, with a broad margin of cells supporting locomotory cilia. The subvelum is a thick ridge of refringent granules covered with short cilia which are in line with and connected to the mouth. Unlike form 1, the metapodium (foot) of form 2 does not possess an operculum and is extremely broad and long, curving around the posterior portion of the shell (Plate 2, B). The foot is granular like the velum and the edge of the sole is fringed with a thick row of these granules; embedded into the tissues at the proximal end is a pair of statocysts.

Although considerably smaller than form 2, form 1 embryos at the late veliger stage also have a fully developed cephalopedal region. The mantle fold which has separated from the lip of the shell allows the embryos to retract into their shells. A columnar (or retractor) muscle is visible as a translucent, fibrous strand positioned on the left side of the embryo. The muscle is inserted into the neck of the left velar lobe and attached to the inside wall of the shell on the left posterior side of the embryo. The bilobed velum of form 1 embryos is thick and each lobe consists of a single row of large refracting marginal cells connected to the head region by epithelial tissue. Like form 2, the marginal cells of form 1 support a dense array of locomotory cilia. Unlike form 2, however, the subvelum is poorly defined with a sparsely ciliated feeding groove on the outside wall of each velar lobe, below the preoral band of ciliated marginal cells. The metapodium is narrow and embedded in the tissue, at the proximal end, is a pair of statocysts. At the distal end of the metapodium, there is a cluster of translucent pedal glands. The sole of the metapodium is covered with short cilia and the upper surface has a transparent operculum attached to it.

Alimentary tract of form 1 embryos at the late veliger stage is similar to that described above for form 2 embryos at the middle veliger stage. Differences do occur in the shape of various organs. The stomach of form 1 is at least twice as large as the digestive diverticula and is kidney-shaped. Like form 2 embryos, the semi-transparent wall of the stomach is composed of refringent granules and the lumen is ciliated. The left digestive diverticulum in form 1 at this stage is more opaque than the right, but is is scarcely larger than the right. A pair of translucent cells, which may be the nephrocysts or secondary kidney, is located in the neck of the cephalopedal region, antero-dorsal to the anus. The entire visceral mass of embryos of both forms at the late veliger stage is enclosed in a perivisceral membrane which separates it from the shell.

Veligers (Plate 2, C and D)

Typical of planktotrophic larvae (Type 1, as defined by Thompson, 1967), the newly hatched veliger larvae of both forms lack eye spots and a propodium. They are positively phototactic and their type 1 shells (as defined by Thompson, 1961) are sinistrally coiled while their asymmetrical bodies are dextrally or hyperstrophically arranged. The shells of form 1 veligers are transparent while those of form 2 are heavily pigmented (Plate 2, C and D).

Mean shell lengths of form 1, form 2 (red-rimmed mantle) and form 2 (jet-black) are as follows: 114 μm, 144 μm, and 153 μm, respectively (Table 1). These shell lengths are significantly different to each other (one-factor ANOVA: $F_{4,45}$=114.7; $P<0.001$). A SNK test indicates that the mean lengths of all form 1 colour morphs are equivalent to each other ($P>0.05$) and less than that of form 2 (red-rimmed mantle) ($P<0.05$), which in turn, is less than that of form 2 (jet-black) ($P<0.05$).

The cephalopedal region of form 2 veligers is at least three times larger than that of form 1. The mean distance between the outside edges of a fully extended velum of form 2 (jet-black variant) is 267 μm (S.D. $\pm$ 12 μm, n = 5). This distance is greater than that found for veligers of *Dendrodoris fumata*, which is 225 μm (Gohar & Soliman 1967).

DISCUSSION

Compared to other *Dendrodoris* species (Table 3), *D. nigra* (form 1) produces high numbers of small planktotrophic eggs per spawn. *D. nigra* (form 2) also produces high numbers of planktotrophic eggs but they are the third largest in diameter. The overall appearance of form 1 veligers is more like that of *D. gemmacea* than like that of form 2. The dark pigmentation of the shell and shape of the cephalopedal region of form 2 veligers are similar to that of *D. fumata*, however, unlike this species, the cephalopedal region of form 2 is much larger, lacks an operculum and is too large to be fully retracted into the shell. In this respect form 2 veligers are similar to the planktotrophic veligers of *Aegires punctilucens* described by Thiriot-Quievreux (1977), except that the cephalopedal region of this species is larger than that of form 2.

Different larval forms produced by colour variants of *Dendrodoris nigra* may indicate that this species is capable of some degree of developmental variability (poecilogony) rather than consisting of two separate species. Widespread species, such as *D. nigra* can have varying developmental patterns associated with different areas of their geographic range. According to Clark & Goetzfried (1978), several sacoglossans and nudibranchs have been shown to have variable development either between or within populations. Eyster (1979) has demonstrated that development within the same population of the aeolid *Tenellia pallida* from South Carolina could be either planktotrophic or non-pelagic (veligers metamorphose inside their capsules before hatching). Clark *et al.* (1979) have shown that development within the same population of the sacoglossan *Elysia cauze* from Florida can vary seasonally, with planktotrophic, lecithotrophic and direct (non-pelagic) development occurring in sequence. West *et al.* (1984) have reported that separate populations of *E. chlorotica* are able to produce either planktotrophic or direct developing larvae.

Cases cited above by these authors, however, involve opisthobranchs which change from one mode of development to another. This does not appear to happen in *Dendrodoris nigra*. Instead, two forms of the same developmental mode are produced. Why should the same species produce two morphologically different larvae that fulfil the same ecological function (i.e., dispersal of offspring)? Adults of *D. nigra* (forms 1 and 2) do not exhibit self-fertilisation like that reported for *Cuthona adyarensis* by Rao (1961). Nor do they change their developmental mode as a result of starvation in the adult like that observed with *Spurilla neapolitana* (Clark & Goetzfried, 1978). Furthermore, neither the size of the adults nor certain extrinsic factors (such as temperature and salinity) could be shown to alter the developmental mode of *D. nigra* from planktotrophy to any of the other modes (Rose, 1981). Consequently, none of the above factors can account for the two larval forms found in different colour variants of *D. nigra*.

According to Eyster & Stancyk (1981) one of the main environmental factors influencing the growth, size and fecundity of the sponge-eating dorid, *Doriopsilla pharpa*, appears to be the abundance of food. Similarly, differences in the egg diameter and number of eggs per spawn found between forms 1 and 2 may be due to differences in the type and amount of food (sponge) associated with the habitat of each colour variant. Differences in larval morphology between forms 1 and 2 suggest that the two forms are adapted for different life cycles. The enlarged velum of form 2 veligers indicates that they may be better suited for longer planktonic periods, or that they may be specialised feeders and stronger swimmers. The transparent larval shells of form 1 and pigmented shells of form 2 may reflect adaptations to different microhabitats by each colour variant of *Dendrodoris nigra*.

Forms 1 and 2 may be sibling species which are sympatric in New South Wales. The lack of observed evidence of copulation in the laboratory between specimen with different developmental patterns and differences between the structure of their spawn, morphology of their larvae and colour of the adults may reflect early stages of speciation. Observed evidence that form 2 veligers are unable to retract into their shell and have a permanently extended, oversized foot without an operculum suggests that forms 1 and 2 have started diverging. According to Gallardo (1977) a similar process is occurring in the prosobranch *Crepidula dilatata* from southern Chile. For this species subtle differences exist in: adult colouration; shape of the egg capsules; egg diameters; spawning seasons; abundance and distribution of adults in the intertidal zone; and differences in developmental types (planktotrophy and direct) (Gallardo, 1977).

Embryological discrepancies and lack of evidence of copulation between specimens with different developmental patterns, suggest that some of the colour variants presenty considered *Dendrodoris nigra* might be sibling species. Before separating these colour variants into different species, however, it will first be necessary to examine in detail the internal morphology of the adults of various colour morphs (especially the reproductive anatomy) and their ecology (habitats, food and reproductive cycle).

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TABLE 1. Collection data and developmental characteristics of *Dendrodoris nigra* (forms 1 & 2). Numerical data are presented as mean ± SD with sample size in brackets. Days to hatching are derived from various egg masses incubated at 22-23°C. Number of egg masses used are shown in brackets.

Development Form														
Colour morph	Locality	Season Collected				Year(s)	Length of Field-collected Animals (mm)	Number of Egg Masses		Eggs/Spawn	Dia. of Eggs (μm)	Dia. of Capsules (μm)	Shell Length at Hatching (μm)	Days to Hatching
FORM 1		Su	Au	Sp	Wn			Field	Laboratory					
WHITE-SPECKLED	LONG REEF	x	x	x	x	1976 1977 1978 1979	54.4 ± 9.9 (8)	4	16	242 000 ± 8 799 (5)	74.6 ± 1.3 (10)	121.4 ± 7.4 (10)	114.2 ± 7.8 (10)	9.6 ± 0.6 (4)
BROWN-BLACK	LONG REEF	x	x	x		1976 1977 1978 1979	57 ± 12 (5)	2	5	240 266 ± 10 000 (4)	73.5 ± 1.6 (10)	121.2 ± 6.1 (10)	113.9 ± 6.2 (10)	9.4 ± 0.2 (2)
GRAY	LONG REEF	x				1979	61 ± 2 (3)	1	1	234 100 (1)	74.3 ± 1.6 (10)	121.6 ± 6.3 (10)	114 ± 6.6 (10)	9.0 (1)
FORM 2														
JET-BLACK	BOTTLE & GLASS CLOVELLY	x	x			1979	65.7 ± 4 (3)	1	5	67 584 ± 21 000 (3)	129 ± 3.0 (20)	162.5 ± 5.0 (10)	152.8 ± 3.1 (10)	9.2 ± 0.7 (2)
RED-RIMMED MANTLE	PILOTS BEACH	x				1979	34 ± 1 (3)	0	1	tens of thousands	121.4 ± 8.1 (43)	140.3 ± 7.1 (10)	144 ± 2.7 (10)	9.3 (1)

TABLE 2: *Dendrodoris nigra* (form 1 & 2). Chronology of developmental stages from oviposition to hatching for 50% or more embryos from several egg masses when incubated at 22-23°C. Times are shown as mean ± SD with number of egg masses in brackets.

DEVELOPMENTAL STAGE	TIME	
	FORM 1	FORM 2
	HOURS	
Oviposition	0	0
Expulsion of 2nd polar body	2.6 ± 0.5 (3)	2.8 ± 0.4 (2)
First cleavage	3.3 ± 0.3 (4)	5.5 ± 0.4 (2)
Second cleavage	5.5 ± 0.6 (4)	9.8 ± 0.5 (2)
Third cleavage	13.0 ± 1.2 (4)	12.3 ± 0.9 (2)
Fourth cleavage	15.3 ± 1.5 (4)	17.0 ± 1.6 (2)
Morula	22.0 ± 1.0 (3)	20.0 ± 1.4 (2)
Blastula	1.2 ± 0.1 (7)	1.0 ± 0.5 (3)
Gastrula	2.2 ± 0.3 (7)	2.2 ± 0.5 (3)
Trochophore	4.1 ± 0.1 (3)	4.1 ± 0.7 (3)
Early veliger	5.1 ± 0.7 (4)	4.1 ± 0.3 (3)
Middle veliger	5.8 ± 0.4 (4)	5.8 ± 0.6 (3)
Late veliger	7.7 ± 0.5 (4)	7.4 ± 0.2 (3)
Hatching	9.6 ± 0.6 (4)	9.2 ± 0.7 (3)

DAYS

TABLE 3: The body length, number of eggs per egg mass, egg diameter and developmental type of species of *Dendrodoris* from various parts of the world. Dash indicates no data.

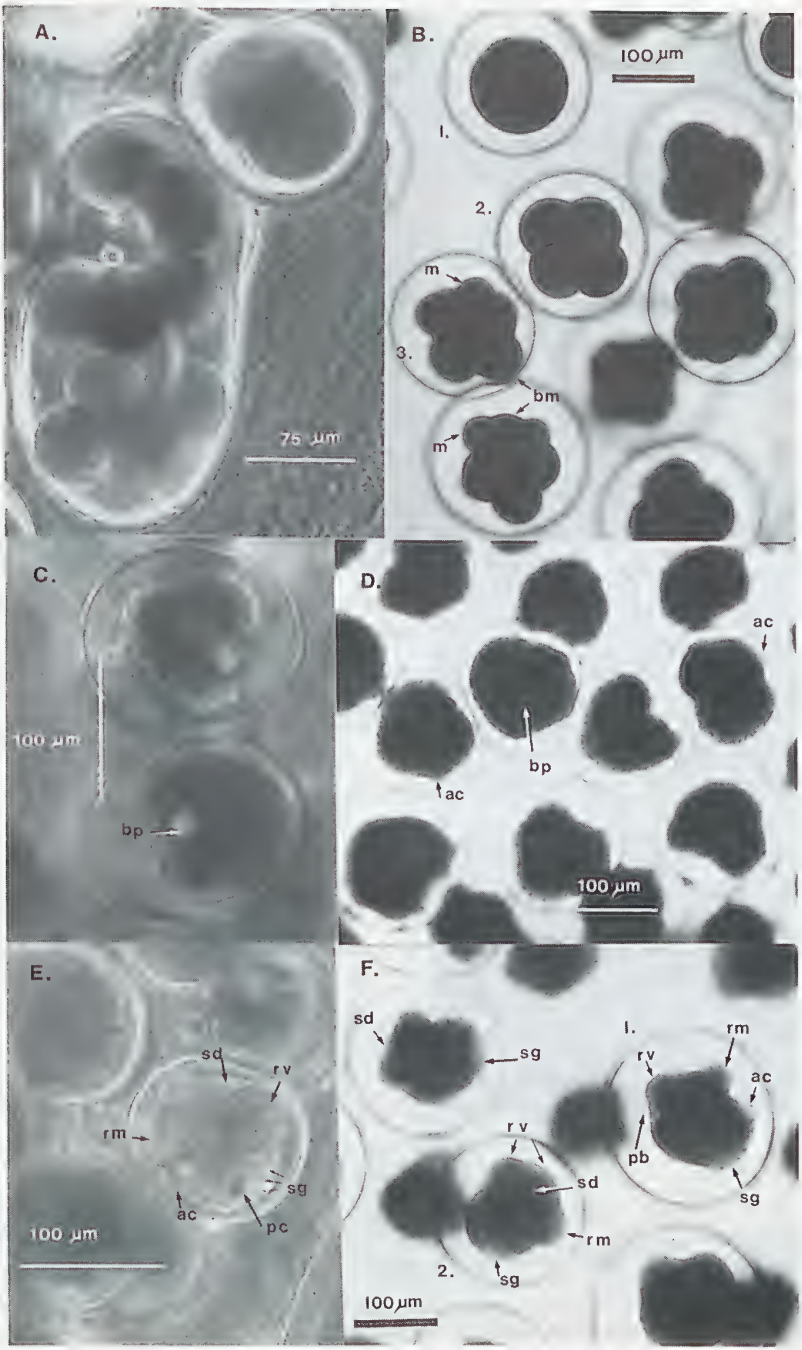
Species	Length (mm)	Eggs per egg mass	Egg dia. (μm)	Dev. type	Reference
Dendrodoris denisoni (Angas)	35-60	2 664	186	direct (non-pelagic)	Rose (1981)
D. fumata (Rüppell & Leuckart)	55	3 344 165 490	100	planktotrophic	Gohar & Soliman (1967)
D. gemmacea Alder & Hancock	60-70	10 000	105	planktotrophic	Rose (1981)
D. krebsii (Mörch)	— —	10,500 —	205 —	direct planktotrophic	Clark & Goetzfried (1978) Bandel (cited by Clark & Goetzfried (1978))
D. nigra (Stimpson)					
form 1	45-70	230 000 251 000	75	planktotrophic	present study
form 2	33-68	46 584 88 600	121-129	planktotrophic	present study

KEY TO LETTERING

anus (a); anal cells (ac); blastomere (bm); blastopore (bp); hindgut loop (hg); larval retractor muscle (lm); left digestive diverticulum (ld); locomotory cilia (lc); metapodium (mp); micromere (m); mouth (mo); operculum (op); pigmented mass of cells (pc); polar body (pb); right digestive diverticulum (rd); rudimentary metapodium (rm); rudimentary velum (rv); shell (sh); shell gland (sg); stomodoeum (sd); statocysts (s); stomach (st); subvelum (sv); velum (v).

PLATE 1

Dendrodoris nigra. A. Form 1 (white-speckled colour variant) : lateral view of embryos at two- and four-cell stage 8 hr after oviposition; note tubular capsule. B. Form 2 (jet-black colour variant) : unfertilised ovum (1.), four-cell stage (2.), and eight-cell stage (3.), 14 hr after oviposition. C. Form 1 (white-speckled) : 2.2 day-old gastrulae with blastopores seen as circular depressions of lightly coloured cells. D. Form 2 (red-rimmed colour variant) : 2.2 day-old gastrulae, note anal cells. E. Form 1 (white-speckled) : left-lateral view of 5.1 day-old early veliger; note darkly pigmented mass of cells. F. Form 2 (jet-black) : right-lateral view (1.) and right-ventro-lateral view (2.) of 5.1 day-old early veligers; note polar body adhering to surface of stomodoeum.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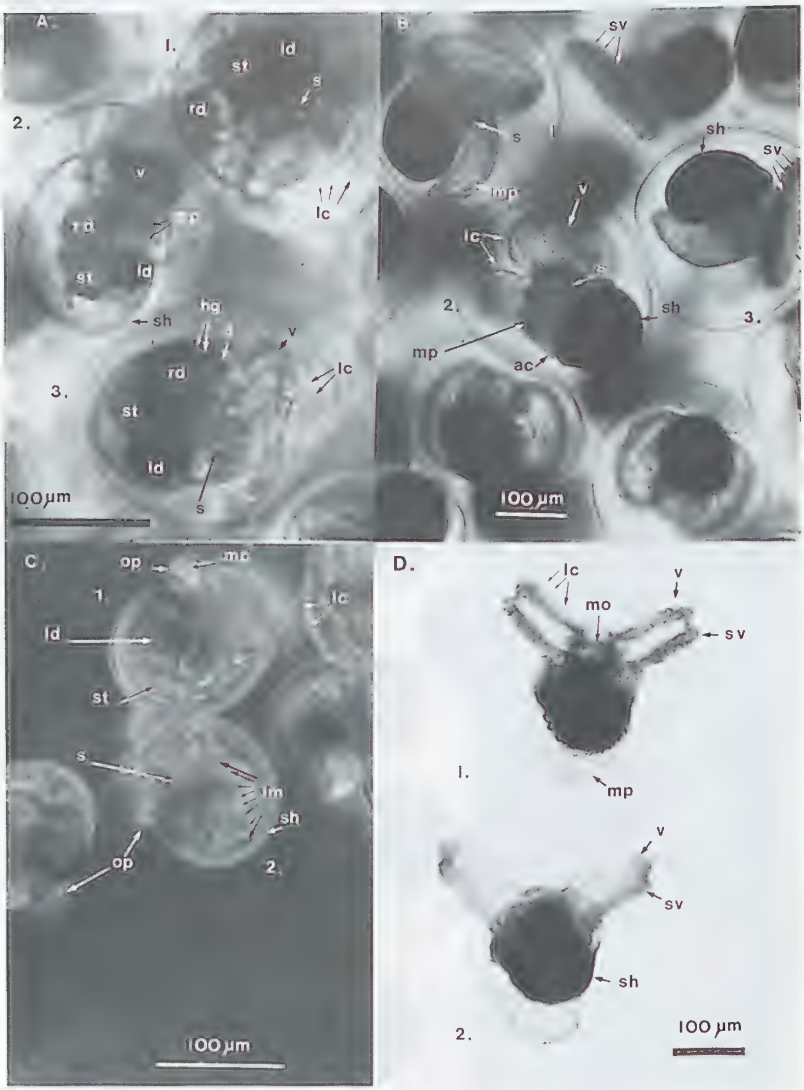

PLATE 2

Dendrodoris nigra. A. Form 1 (white-speckled colour variant) : left-lateral view (1.), right-ventro-lateral view (2.) and ventral view (3.) of 7.3 day-old embryos at late veliger. B. Form 2 (jet-black colour variant) : right-lateral view (1.), postero-ventral view (2.) and right-lateral view (3.) of 7.4 day-old embryos at late veliger. C. Form 1 (white-speckled) : left-ventro-lateral view (1.) and left-lateral view (2.) of newly hatched veligers 9.6 days after oviposition. D. Form 2 (jet-black) : ventral view (1.) and dorsal view (2.) of newly hatched veligers 9.2 days after oviposition.